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alike, or they may be very different from each other. A grain of corn homozygous for yellow starch and red aleurone is different in color from one having only one of these characteristics. But to a person with defective vision, or when viewed in a light of proper color, these two colors and a combination of the two may appear to be merely different shades of one color. By breeding this stock with a homozygous white, carrying no conflicting factors, we should get what would be to this same defective vision a perfect illustration of the behavior of multiple factors. But it is in reality a case of dihybridism in which we have failed to distinguish between the two sets of allelomorphs. And who can doubt that relatively as great a lack of discrimination may characterize our chemical, physical, or morphological vision in observing some of the classical illustrations to which the multiple factor hypothesis is applicable?

Other examples could be selected from the work that has been done on maize, and doubtless many are available from the investigations made with other plants and with animals, but these will suffice for illustration. Many of the organisms most useful for establishing and testing principles of heredity have an external appearance that may be very deceptive as an indicator of their true structure, and the true structure alone is the key to the deeper significance of their genetic behavior.

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ON HETEROPHYLLY IN WATER PLANTS

THE occurrence of two or more different types of leaf upon one individual, which is so frequently characteristic of water plants, has long attracted the interest of botanists. The most usual case is that in which the submerged leaves are finely divided while the floating or aerial leaves are relatively simple. Lyte's Herbal (1578) contains a vivid description of this type of heterophylly in the water buttercup. Since this description is also noteworthy for its insistence on the influence of external conditions, it may be cited here.

Amongst the fleeting [floating] herbes, there is also a certayne herbe whiche some call water Lyverworte, at the rootes whereof hang very many hearie strings like rootes, the which doth oftentimes change his uppermost leaves according to the places where as it groweth. That whiche groweth within the water, carrieth, upon slender stalkes, his leaves very small cut, much like the leaves of the common Cammomill,

but before they be under the water, and growing above about the toppe of the stalkes, it beareth small rounde leaves, somewhat dented, or unevenly cut about. That kind whiche groweth out of the water in the borders of diches, hath none other but the small jagged leaves. That whiche groweth adjoyning to the water, and is sometimes drenched or overwhelmed with water, hath also at the top of the stalkes, small rounde leaves, but much more dented than the round leaves of that whiche groweth alwayes in the water.

Among certain Nymphæaceæ we find a different type of heterophylly in which the submerged leaves are large, thin and translucent, somewhat resembling the seaweed *Ulva*. These leaves are particularly well shown in the yellow water-lily.

To enumerate all the varieties of submerged leaf met with among angiosperms would be too long a task to undertake in the present paper. It must suffice to say that they are either highly divided, ribbon-like, or else thinner and broader than the corresponding air leaves. They are characterized anatomically by the lack of stomates and by the presence of chlorophyll in the epidermis. They are thus well suited for the absorption of carbon dioxide in the dissolved form in which it presents itself to water plants.

In considering the significance of heterophylly, it is a matter of importance to remember that the occurrence of different leaf-forms in a single individual is not confined to aquatics but occurs also in terrestrial plants. Nehemiah Grew, as long ago as 1682, pointed out that in many cases one plant bears leaves

of Two Kinds or Two distinct *Figures*; as the *Bitter-sweet*, the common *Little Bell*, *Valerian*, *Lady-Smocks*, and others. For the *Under leaves* of *Bitter-Sweet*, are Entire; the Upper, with two *Lobes*: the *Under Leaves* of the *Little Bell*, like those of *Pancy*; the Upper, like those of *Carnation*, or of *Sweet William*.

We find parallels to the heterophylly of hydrophytes, not only among terrestrial flowering plants, but also in the case of the distinct "youth forms" of conifers, and even—more remotely—in the "*Chantransia*" stage of such algæ as *Batrachospermum*. Heterophylly is indeed so widespread that no interpretation can be valid unless the condition be treated broadly as a very general attribute of plant life, rather than as a rare and exceptional phenomenon, for which special and individual explanations will suffice.

To the earlier writers, such as Lamarek, the problem of heterophylly presented no difficulties. They regarded the submerged or aerial type of leaf as representing a direct response, on the

part of the plant, to the medium. The work of the last thirty years has, however, rendered this simple conception untenable; the theory that now holds the field accords a much less prominent place to adaptation. The first observation that shook the foundations of the idea that leaf form necessarily depended directly on the milieu, was that of Costantin, who showed that, in the case of *Sagittaria*, the aquatic and aerial leaves were already differentiated from one another in the submerged bud; he noticed auricles on a leaf which was only 2 to 3 mm. long. In *Ranunculus heterophyllus*, also, the leaves destined to be aerial are differentiated in the bud.

A large amount of experimental work has been published by various authors on the effect of conditions upon the leaf forms of heterophyllous plants, and, although some of the results are confused and conflicting, a study of the literature seems to justify one general conclusion—namely, that, in many cases, the submerged type of leaf is, in reality, the juvenile form, but can be produced later in the life history in consequence of poor conditions of nutrition; the air leaf, on the other hand, is the product of the plant in full vigor and maturity. This conclusion, which is primarily due to Goebel and his pupils, is substantiated not only by experiments but by observations in the field.

In many heterophyllous plants, the first leaves produced by a seedling, whether it develops on land or in water, conform, more or less, to the submerged type. This is the case for instance, in the Alismaceæ. In *Alisma plantago*, the water plantain, and *Sagittaria sagittifolia*, the arrowhead, the first leaves produced by the seedling (or the germinating tuber) are ribbon-like, even when the young plant is terrestrial. The formation of this type of leaf can be induced again, even in maturity, by conditions which cause a general weakening of the plant. Costantin thirty years ago, recorded that, when the leaves of *Alisma plantago* were cut off in the process of clearing out a water course, or in a laboratory experiment, the next leaves produced were ribbon-like, thus representing a regression to the submerged form. More recently, another worker, Wächter, tried the experiment of cutting off the roots of healthy, terrestrial plants of *Sagittaria natans* bearing leaves with differentiated laminae. It was necessary to cut the roots away every week, as they grew again so rapidly. The result of this treatment was that the plants were found to revert to the juvenile stage, the new leaves being band shaped. When the experimenter ceased to interfere with the roots, the plants again formed leaves with laminae. Other plants,

with uninjured roots, grown as water-cultures in distilled water, also produced the juvenile leaf form, while those grown in a complete culture solution developed their laminae normally.

The same observer recorded a case in which a plant of *Hydrocleis nymphoides* Buchenau (Butomaceae), which had been bearing the mature form of leaf, was observed to revert to the ribbon form. On examination it was found that most of the roots had died off. When a fresh crop of roots was produced, the mature type of leaf occurred again.

Another writer, Montesantos, showed by a series of experiments upon *Limnobium Boscii* (Hydrocharitaceae) that, in this case also, the heterophylly is not a direct adaptation to land or water life, but that the floating leaves are "Hemmungsbildungen" due to poor nutrition. In the water soldier, *Stratiotes aloides*, also, he showed that the stomateless leaves were primary, but that their production could be induced at later stages by unfavorable conditions.

An experiment tried by Goebel on *Sagittaria sagittifolia* indicated that absence of light in this case inhibits the formation of leaves of the aerial type. An observation of Glück's on *Alisma graminifolium* Ehrh., also points to the same conclusion. But it seems probable that the effect produced in these cases was not due directly to the darkness, but to the state of inadequate nutrition brought about by the lack of light for carbon assimilation.

Among the potamogetons, again, experimental work by Esenbeck has shown that reversion to juvenile leaves can be obtained under conditions of poor nutrition. For example, when a land plant of *P. fluitans*, which had been transferred to deep distilled water, had its adventitious roots repeatedly amputated, regression was obtained to the floating type of leaf and then the submerged type. A similar reversion to thin narrow leaves was brought about in the case of *P. natans* by growing the upper internodes of a shoot as a cutting.

Water lily leaves respond to experimental treatment in just the same way as the monocotyledons already mentioned. In the case of two species of *Castalia*, it has been found possible to induce the mature plants to form submerged leaves, either by removing the floating leaves or by cutting off the roots. This confirms an earlier suggestion, made by an Italian writer, Arcangeli, that the development of the submerged leaves of *Nymphaea lutea* was due to "un indebolimento o diminuzione di energia vitale." This suggestion has received independent, experimental confir-

mation from Brand, who estimated that a well-developed floating leaf of *Nymphæa lutea* was about eleven times the dry weight of a submerged leaf of the same area.

Another dicotyledon, *Proserpinaca palustris*, which was investigated by Burns, gave experimental results pointing to the same general conclusion as those already quoted. The primitive type of leaf in this plant is always a "water" leaf, but this type of leaf was also produced in the autumn by all the plants, regardless of any external conditions which the experimenter could control. On the other hand, at the time of flowering and in the summer generally, almost every plant, whether growing in water or air, produced the "land" type of leaf—the transition from the "water" to the "land" type taking place earlier on strongly growing than on weak stems. The author considers it evident that the aquatic environment is not the cause of the division of the leaf, nor does it depend on light, temperature, gaseous content of the water or contact stimulus. The only conclusion which he holds to be justified by his experiments is that *Proserpinaca palustris* has two forms, an adult form and a juvenile form; under good vegetative conditions, it tends to produce the adult form with the undivided leaf, the blossom and the fruit, while, if the vegetative conditions are unfavorably influenced, a reversion can be induced to the primitive form with the submerged type of leaf. These results are consistent with those of McCallum, who had dealt with the same species at an earlier date, but his interpretation is slightly different. He is inclined to regard the occurrence of the water form as induced by the checking of transpiration and the increased amount of water which hence accumulates in the protoplasm. This explanation is not inconsistent with the more general view that any condition tending to lower the vitality may be responsible for a reversion to the submerged type of leaf.

In nature, the regression to the juvenile type of leaf sometimes occurs, not only in the case of an entire plant subjected to adverse conditions, but also in the case of lateral shoots from an individual which is otherwise producing the mature form of leaf. Goebel for instance, examined an old example of *Eichhornia azurea* (Pontederiaceæ) which had wintered as a terrestrial plant in a greenhouse; the leaves were of the mature form, differentiated into sheathing base, petiole and lamina, except in the case of a lateral shoot, which, on the contrary, bore the grass like, simple leaves which characterize the young plant. Goebel also

describes the occurrence of subdivided leaves of the water type on lateral shoots of normal land plants of *Limnophila heterophylla*. A corresponding reversion has been observed in the case of the side branches of plants of *Proserpinaca palustris* developing *in the air* from a plant whose main stem was producing the mature type of leaf; by removing the growing apex of the stem in June, side branches of the "water type" were induced to develop.

The interest of these lateral shoots, which show a reversion to an *ontogenetically* earlier type of leaf, is enhanced by the fact that C. and F. Darwin in "The Power of Movement in Plants" have recorded a case of the occurrence, on lateral shoots, of leaves whose characters are probably *phylogenetically* earlier than those which the species normally exhibits. Their observations related to the sleep habits of the allied genera, *Melilotus* and *Trifolium*. They noticed in *Melilotus Taurica* that leaves arising from young shoots, produced on plants which had been cut down and kept in pots during the winter in a greenhouse, slept like those of *Trifolium*, with the central leaflet simply bent upwards, while the leaves on the fully grown branches of the same plant afterwards slept according to the normal *Melilotus* method, in which the terminal leaflet rotates at night so as to present one lateral edge to the zenith. They suggest that *Melilotus* may be descended from a form which slept like *Trifolium*.

The idea that the "juvenile" leaves produced on lateral shoots may in some cases represent an ancestral type, is consistent with the facts in the case, for instance, of the Alismaceæ, provided that the "phyllode theory" of the monocotyledonous leaf be accepted in the sense advocated by Professor Henslow and the present writer. According to this theory, the ancestral leaf of this family was ribbon-shaped, while the oval or sagittate blade (or "pseudolamina") represents a later development—a mere expansion of the apex of the petiole. The submerged youth leaves of this family would thus represent a reversion to phylogenetically older forms.

If the interpretation of heterophylly indicated in the present paper holds good at all widely, the teleological view of the submerged leaf must be considerably modified. The present writer would like to suggest that, for the old conception of heterophylly as *induced* by aquatic life, we should substitute the idea that such a difference between the juvenile and mature forms of leaf as would render the juvenile leaf well suited to aquatic life, has been

in many cases one of the necessary preliminaries to the migration from land to water, and that the aquatic angiosperms thus include, by a process of sifting,¹ those plants whose terrestrial ancestors were endowed with a strong tendency towards heterophylly.

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COALESCENCE OF THE SHELL-PLATES IN CHITON*

CHITONS are peculiar in the fact that the molluscan shell is here represented by a series of eight distinct dorsal plates, which in different genera overlap and articulate with one another to varying degrees. The full number, 8, seems, however, to be invariably present. While examining recently a series of somewhat over 2,100 individuals of *Chiton tuberculatus* L., I came upon two cases, and two only, exhibiting any irregularity with respect to the number of the shell-plates. These were specimens, a male and a female, found near together on the beach at Cross Bay, Bermuda, in which plates 7 and 8 had in each instance almost completely fused (Figs. 2-6), so that each of these animals seemed at first sight to have but 7 plates; since no records seem previously to have been made of such occurrences, they are here figured and described.

In the two abnormal chitons the fused terminal plates were of similar external appearance, but in individual A, the female, the coalescence of plates 7 and 8 was somewhat less complete than in individual B, the male, as shown by the form of the inner surfaces of the compound plates. It is perhaps accidental that in both cases fusion of the respective plates is somewhat assymetrical, being more complete on the right side. As seen in Fig. 4, the muscular intersegmentum, which ordinarily receives the insertion plates of the eighth valve, is represented by a relatively small tongue of tissue.

¹ We owe to Dr. H. B. Guppy, F.R.S., the important idea that the habitats of plants are determined by their peculiarities of structure and not *vice versa*. In relation to the occurrence of plants with buoyant seeds and fruits in water-side stations, he writes, "there are gathered at the margins of rivers and ponds, as well as at the sea-border, most of the British plants that could be assisted in the distribution of their seeds by the agency of water. This great sifting experiment has been the work of the ages, and we here get a glimpse at Nature in the act of selecting a station."

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